REFLEXES ELICITABLE IN THE CAT FROM PINNA VIBRISSÆ AND JAWS. By C. S. SHERRINGTON.

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CONTENTS.

I. Reflexes of the Pinna.

The aural pinna of the cat, sensitive and mobile as it is, yields a number of reflexes. One of them has been briefly referred to by me before (18, 19): I know no other reference to them, although doubtless they have been met by other observers. For the following experimental examination of them the animal was deeply chloroformed and then decerebrated with the decerebrator (13, 20). The decerebrator was so adjusted that the head was removed inclusive of fore-brain and mid-brain, the transection passing close behind the posterior colliculi and close in front of the Gasserian ganglia and the third divisions of the trigeminal nerves.

By drawing the pinnæ well back when the head is guillotined these can be left attached to the carcase and their reflexes then examined. The narcosis being relaxed, the examination of the reflexes was begun usually about an hour later.

In this way the reflex movements elicitable from the pinna are found to be in the main five in number. These, to distinguish them, may be termed (1) the retraction reflex, (2) the folding reflex, (3) the head-shake reflex, (4) the cover reflex, (5) the scratch reflex, this last being the already-studied reflex in which the ipsilateral hind-foot is brought forward to scratch the stimulated part.

1. *The retraction reflex.*

The reflex movement is one which swings the pinna backward, rotating it about an axis which runs transversely through the head approximately from one auditory meatus to the other. It resembles the movement which a cat makes commonly when one attempts to handle the pinna. In the decerebrate preparation I have seen it aroused by the settling of a fly upon the ear. When brisk and brief, as it is often, it recalls a movement of the pinna seen in cattle worried by flies about the head, but in them the backward movement is usually succeeded by a forward one more immediately than in the cat. It is not always brief; if the stimulus be strong or maintained the pinna is for a time kept retracted. The pose of the pinna is then such as it often assumes in anger or defence. Darwin (6) furnishes a figure of this posing of the ear as a characteristic expression of emotion in a cat threatened by a dog. A principal muscle acting in this reflex is the lateral portion of levator auris longus, as is ascertainable by direct inspection of the exposed muscle. The motor nerve is facialis.

Receptive-field. Before attempting to describe the receptive skin-field whence stimulation evokes the reflex, a brief reference to some anatomical features of the cat's pinna may be helpful (Fig. I, 1 and 2).

The trumpet-shaped organ is divisible into two main parts whose concavities conjoin. The upper less concave is the *scapha*, the lower, resembling a smaller and deeper spoon-bowl, is the *concha*. The external auditory meatus lies at the proximal attached base of this latter. Where the pinna joins the cheek the ridge of skin which juts up as a fold in front of the meatus has two notches in it instead of the single one of the human ear; of these the lateral rather than the medial gives more direct access to the *meatus*. The names given to the three parts of this ridge are, in the medio-lateral direction, *tragus*, *intertragus*, and *posttragus*; two notches or *incisuræ* lie between them.

The scapha at the more proximal part of its latero-ventral border has a deep notch, and around that a rather large lateral extension, the *bursella* or pocket. Each edge of the notch is developed into a lappet and from these run ridges extending downward within the concave face of the scapha and these ridges continue into the concha and are directed toward the meatus. Apart from these the concave face of the scapha is practically smooth. On the other hand, the concave face of the concha has a number of pronounced ridges and projections. Of these latter the chief are the *wart* or *supratragus* (Mivart (14), *antihelix* Reichard and Jennings (15)) which lies high up near the scapha, and the two

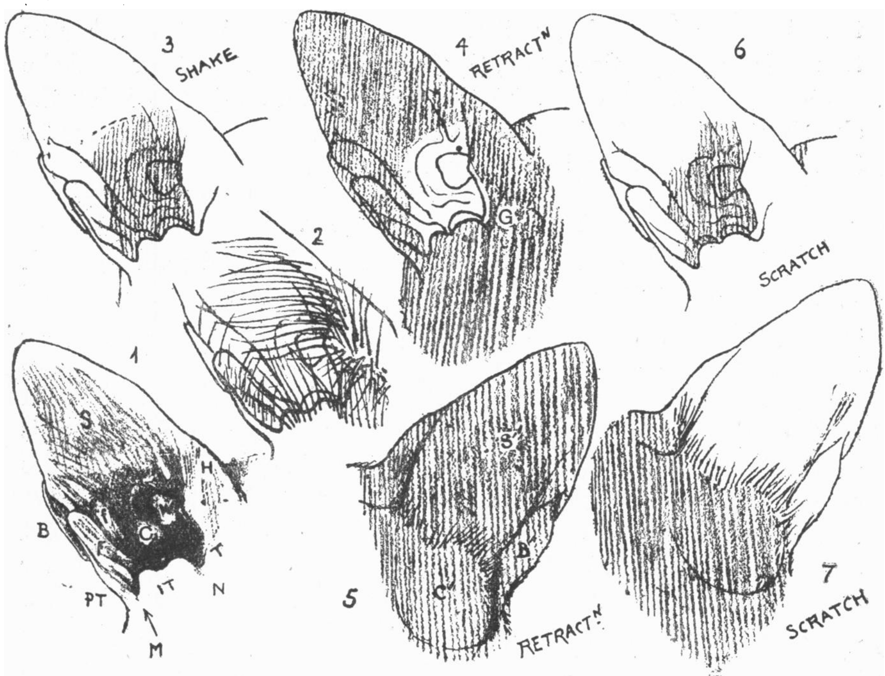

Figure I. 1. Front aspect of the shaven pinna. *S*, scapha; *C*, concha; *B*, bursella; *f*, *F*, lappets from bursella to concha; *T*, *IT*, *PT*, tragus, intertragus, and posttragus; *W*, supratragus ('wart'); *H*, helix; *M*, *N*, incisuræ; the tops of the 'cushions' are seen projecting from ampulla beyond intertragus; the crescent is seen partially surrounding *W*, the supratragus. 2. indicates the arrangement of the guard-hairs. 3. the receptive-field of head-shake reflex: the broken line marks the position of the 'crease' where the folding in the folding-reflex occurs. 4, 5. Receptive-field of the retraction reflex seen from front and back respectively; *G*, the hairless trigone of low threshold. *S'*, *B'* and *C'* convex surface of scapha, bursella, and concha. 6, 7. Receptive-field of scratch-reflex from front and back. The extent of the receptive-field is in each case shown by the line-shaded area.

'*cushions*' large pearl-like eminences low down in the concha. Between the cushions is a deep grove leading direct to the meatus.

The chief ridges in the concha are: (1) the downward continuations of the folds from the upper and lower lappets of the bursella, that from the lower lappet joining the lateral cushion guarding the auditory meatus; (2) the *crescent*, a curved ridge like a vallum bordering the fossa which nearly encircles the supratragus; (3) a small ridge which runs towards and finishes in a little peak close above the supratragus; sometimes this has two other small isolated peaks in its upper part. Below the crescent is the deepest part of the concha, the *ampulla*.

A *helix* such as exists in the human pinna exists in the cat's ear only along the proximal part of the oral, *i.e.* medial border, of the pinna.

From the posterior surface of the pinna the scapha is obvious enough, bearing the bursella, but the concha lies buried from view in the deep fur of the neck. When the neck and side of the head have been shaved the concha stands out as a bold convexity shaped as indicated in Fig. I, 5. Short, fine hairs clothe the concavity and convexity of the scapha including the bursella; but in certain regions the hair is of a different character consisting of much coarser longer hairs more sparsely set: these, in view of the experimental findings, may be called guard-hairs They belong to the helix, part of the tragus, the intertragus, posttragus, and the bursella lappets. From all these places they slope so as to fence across the concavity of the concha and also, although to a less extent, of the scapha. Their position and manner of intercrossing is indicated diagrammatically in Fig. I, 2. On the back of the pinna the hair although short on the scapha, changes to deep fine fur over the concha similar to and continuous with the deep fur of the neck; the line where the deep fur ends as a sort of fringe at the back of the base of the scapha is shown in Fig. I, 7. This long fine fur although long does not at all resemble the guard-hairs above mentioned on the front face of the pinna.

The skin of the incisura and its groove between tragus and intertragus is devoid of hair, and almost so is a triangular patch of skin adjoining it (Fig. I, 4 *G*). Throughout the concavity of the concha the skin is hairless.

The receptive-field of the retraction reflex (shaded area in Fig. I, 4 and 5) extends over the whole of the posterior, convex face of the pinna, and over the larger part of the anterior, concave face as well. In this latter it includes the whole of the scapha, bursella, posttragus, intertragus, and helix, and also the part of the concha where run the ridges descending from the bursellar lappets. But it does not include the deep proximal part of the concha nor the 'wart' and 'cushions' nor the auditory meatus itself. It further extends over a small zone of the scalp bordering the pinna, and over a broad strip of the cheek in front of the tragus, and below and in front of the whole attached root of the pinna; the cheek-field of the reflex reaches from the root of the pinna to nearly half-way to the angle of the mouth in one direction and nearly half-way to the outer canthus of the eye in another.

The receptive field is therefore ring-shaped around the actual orifice of the ear, the width of the ring-like strip being greatest behind the orifice. As regards the relative sensitivity of the various parts of the field, the reflex can be so readily evoked from such a great extent of the field that a focus can hardly be said to exist. And, during any prolonged examination of the field, the greatest sensitivity often seems to be now in one part now in another, quite unlike the constant focus met with in most reflexes. A small region of distinctly low threshold is, however, the triangular almost hairless patch (Fig. I, 4 *G*) in front of incisura medialis. Also the extreme edge of the field exhibits, generally speaking, higher thresholds than elsewhere.

Stimuli. The adequate stimulus is clearly mechanical in nature. The lightest touching of a hairlet projecting from the pinna tip will usually evoke the reflex. A hair æsthesiometer of less than 2 mgm. power applied to any one of many points in the field is commonly sufficient. A light puff of air on the scapha also often suffices. A fly alighting on the pinna of the preparation will excite the reflex violently.

All mechanical stimuli are not equally effective. When the reflex excitability is not high direct pushes, *e.g.* with the blunt end of a pin, the hairs being avoided, often fail to evoke the reflex, although the slightest touch of a hairlet or of the longer guard-hairlets practically unfailingly provokes it. When a hairlet or guard-hair is held with fine forceps and pulled on as if to uproot it, the reflex is usually not evoked. The hairlets slope and lean across rather than project vertical to the plane of the receptive surface. It would seem that the essentially adequate stimulus for the reflex is any mechanical disturbance of the hairs which tends to cause sidewise displacement of their roots. Nerve-endings connected closely with the hairs evidently furnish a large proportion of the receptors which evoke the reflex, and the hairs in question include not only hairlets and guard-hairs of the pinna but those of the ordinary fur as well behind the back of the pinna and above it and on the cheek. But other receptors in addition to those of the hairs must also contribute to the reflex. This seems clear from the following facts: (1) light touches, *e.g.* with the end of cotton thread 15 cm. long, excite the reflex readily from the carefully shaven ear; (2) the reflex is excitable similarly by touches on the hairless trigone in front of the medial incisura; (3) more rarely the reflex is elicited by touching lightly the cushions and the ampulla; when the ear has been carefully shaven this is possible without complication of any touch elsewhere and even the cotton thread will sometimes suffice to excite the reflex from a cushion. The reflex then usually but not always is accompanied by the head-shake reflex; (4) the reflex can also be elicited by a faint stream of air directed upon the concave face of the shaven pinna.

Ordinary modes of electrical stimulation evoke the reflex with great difficulty and uncertainty (19). Faradic stimulation, by means of a minute entomological gilt pin used as stigmatic electrode by the unipolar method, is fairly effective for evoking the scratch reflex, but it has uniformly failed to evoke this reflex.

The following devices were adopted in order to escape the difficulty that the mechanical application of any ordinary electrode, even the lightest wire, itself excites the reflex and twitches off the electrode. To one of the hind-feet a broad copper plate and wet pad of cotton-wool soaked in strong saline was bandaged against the skin of the pad and cushions. A cotton thread about 50 mm. long was attached to the end of the single wire platinum electrode and was soaked in strong saline. Where hairlets are few and short, for instance on the mid concavity of the pinna, a droplet, about a 3 mm. bead, of strong salt solution was gently placed: this can sometimes be done without exciting the reflex. The end of the cotton thread as stigmatic electrode was then brought to dip into the bead of saline. The short-circuiting key was then opened by an assistant. The current so applied even when strong enough to cause contraction of some of the small muscles of the pinna and to evoke reflex closing of the eyelids and movement of the vibrissæ and sometimes of the limbs, would yet time after time fail to evoke the reflex retraction of pinna. It was found that with a longish and light cotton thread, the mechanical touch of the wet thread was often insufficient to evoke the reflex and the observation could then be made without the bead of saline. Only on very few and rare occasions did faradisation evoke the reflex although effectively evoking other reflexes.

The one mode of electrical stimulation which has been fairly successful has been the brush discharge of a high-frequency apparatus delivered from a knob electrode approached near to but not of course touching the pinna. This, when approached similarly to the back of one's own hand, gave a hardly perceptible faint coolish tickling sensation.

Afferent nerves. Behind and below the pinna the great auricular nerve as followed forward toward the pinna breaks up into three branches on the parotid gland. The two more ventral of these do not yield the reflex, but the dorsal yields it, and so does each of the branches into which this soon divides. The main trunk of the great auricular as followed back past its crossing with spinal accessory also continues to yield it although not so certainly, the reflex becoming swamped by other effects produced by the main trunk. Another and much smaller nerve-trunk also yields the reflex, this is the dorso-median division of the occipital nerve coming from the 1st and 2nd cervical nerve-roots. But the reflex is not so regularly and well obtainable from this nerve as from the great auricular. The lateral division of the occipital nerve has not yielded the reflex.

To evoke the reflex from these nerves mechanical stimulation is much more effective than is electrical. Electrical stimulation of them usually fails to give the reflex. On the other hand, mechanical stimulation evokes it with great facility. Not only does the ligating of the nerve evoke the reflex with practical constancy, but the lightest, almost imperceptible pull by the thread attached to the ligated nerve. Faradism failing, therefore, I have used a small wheel tetanomotor for observing the frequency at which under repeated mechanical stimuli the brief flick reflex becomes a steady maintained one. The highest rate I could attain with the tetanomotor was 16 per sec. and with this rate the reflex movements though partially fused were still not steady; the pinna was retracted but in that posture maintained a quick regular flickering motion somewhat like that of an insect's wing. The observation shows that in this reflex there can be no long-lasting refractory phase such as obtains in the scratch reflex (21) and the swallow (29, 13). Moreover the reflex when elicited by a strong mechanical stimulus is often a prolonged one, the retracted posture being steadily maintained even for several seconds after withdrawal of the stimulus; it then sometimes becomes tremulent before dying out.

Afferent nerve-roots. The nerve-roots subserving the reflex, *i.e.* the roots which contribute to the entrant path of the reflex into brain and cord, I have determined in two ways: (1) mechanical stimulation of the respective roots, (2) method of 'remaining æsthesia.' Mechanical stimulation, applied to the bared root itself, has yielded the reflex in the case of the following roots: (1) trigeminus, (2) vagus (the two posterior filaments of the root only were effective), (3) the 1st cervical, (4) 2nd cervical, and (5) 3rd cervical. In employing the method of remaining æsthesia the whole series of cranio-spinal nerve-roots between trigeminus in front and 4th cervical behind, inclusive of these, were severed in the cranio-vertebral canal excepting only in each experiment that particular root whose skin distribution as regards the pinnal reflexes it was desired to examine. The receptive-fields of the retraction reflex and of the other pinnal reflexes were then explored for that remaining root. For the exploration the suitable punctiform stimuli, chiefly mechanical, were used, and a point to point examination made. The results obtained were charted on previously prepared maps of the pinna and adjacent surface as the observations proceeded.

Fig. II exhibits the delimitations of the nerve-root skin-fields of the pinnal region as revealed in the above-mentioned way. A detailed verbal description of them seems unnecessary here, the figure making clear their extents and borders better than can description in the text. Later in this paper, after the several pinnal reflexes have been dealt with, reference will be made to these root-fields again, in connection with their relation to the receptive-fields of the several reflexes themselves.

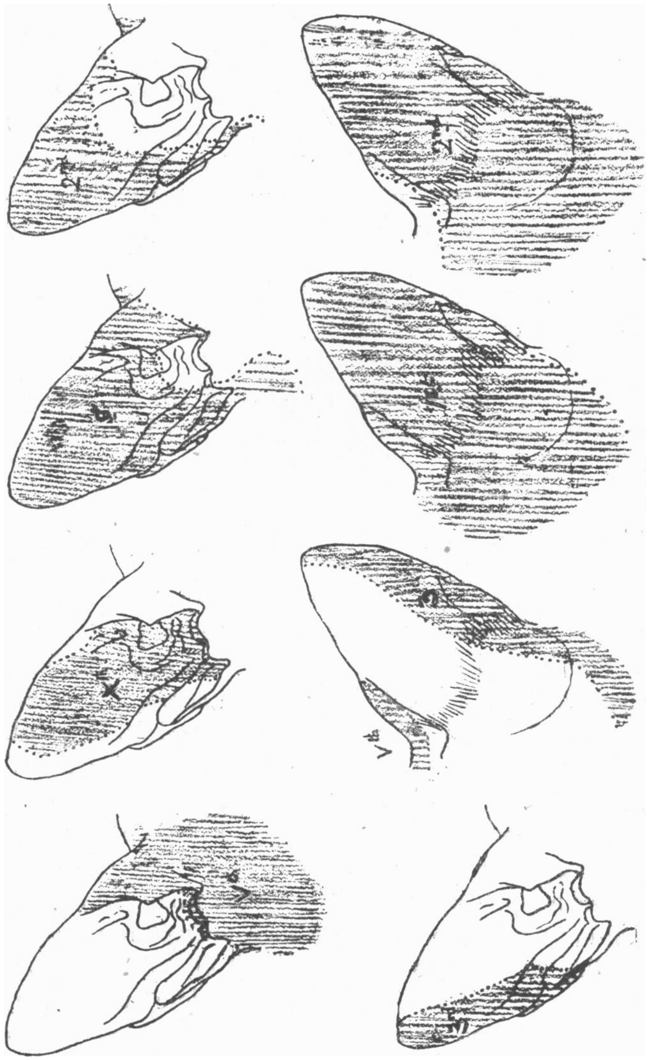

Figure II. Skin-fields of the afferent nerve-roots supplying the pinnal region. v^{th}, trigeminus; x^{th}, vagus; 1st, 2nd, 3rd, first, second and third cervical afferent roots.

2. *The back-folding reflex.*

When the pinna is strongly stimulated, as by compressing the tip between finger and thumb there is evoked a folding of the upper part backward and downward. From the inside of the pinna there can be seen a slight crease (shown by broken line in Fig. I, 3) running transversely in a slight curve across it somewhat above the level where concha and scapha meet. It is at this crease that the folding is effected. The muscle which mainly produces the folding is a delicate sheet *transversus auriculae* easily exposed by removing the skin from the back of the pinna. In Darwin's(6) figure above referred to the back-folding action is depicted, along with retraction, as part of the postural play of the ear in the emotion of fear and anger. In the reflex preparation also it frequently accompanies the retraction reflex; but it is also often elicited apart from this latter, as is the latter apart from the folding. Its movement although brief to a weak stimulus is usually prolonged in response to strong stimulus, sluggishly dying out, often with a tremor, long after withdrawal of the stimulus. The motor nerve is *facialis*.

The receptive-field resembles closely that of the retraction-reflex. For that reason no separate figure of it is given, but it is less extensive than the latter, extending hardly at all to the cheek or neck or scalp nor to the lower part of the back of the concha. In short, it seems confined to a field on the pinna itself and there to be conterminous or nearly so with that of the retraction reflex.

The stimuli appropriate for it resemble closely those adequate for the retraction reflex. Touches excite it. A touch on a hairlet will evoke it, or a touch given by a long cotton thread even on the cleanly shaven scapha. A light puff of air directed through a small tube excites it often more readily than the retraction reflex. Faradisation applied through a moist cotton thread is less ineffectual for it than for the retraction reflex.

As mentioned above it often accompanies the retraction reflex, and this commonly occurs as follows. A light touch *e.g.* on the shaven pinna which at each repetition is evolving a twitch-like retraction reflex, when increased or when prolonged excites the crumpling reflex in addition. The settling of a fly on the pinna will do this: the retraction reflex flings the fly off and the longer lasting folding-reflex keeps the pinna withdrawn, avoiding as it were its being alighted upon again. When obtained from the concavity of the scapha adjoining the concha it is occasionally accompanied by the head-shake reflex.

The afferent fibres for the reflex run in the vagus and 1st, 2nd and 3rd cervical nerves respectively; that is, the reflex is still obtainable, in so far as its field lies within the field of each of these nerves, when any one of these nerves remains uncut, all the rest of this cranio-spinal series of nerve-roots supplying the ear having been severed.

3. *The head-shake reflex.*

In the decerebrate cat a rapid rhythmic shaking of the head is provoked by inserting a little fluid into the concha, a single drop of water often suffices. The movement resembles the shaking of the head given by a dog on coming out of water. The movement consists in alternate right and left rotations of the head about its long axis. In the reflex as observed in the decerebrate cat the opening phase of the movement is in the sense that when seen from the front of the animal the rotation as evoked from the right ear is anti-clockwise, from the left ear clockwise. A movement of closure of the eyes often accompanies the shake of the head. The movement is even in the decerebrate preparation extremely effective in freeing the ear of a drop of water: I have seen it throw out even a light wisp of cotton wool placed in the concha.

The reflex is evocable by other means as well as fluid. A puff of air directed into the pinna gives it. If the puff is directed through a small tube this stimulus excites the retraction reflex of the pinna or the crumpling reflex or both when turned to the scapha either back or front, but excites the head-shake reflex when turned into the concha or meatus. Mechanical touches applied to the inner face of concha or meatus also excite it: this supplies a means of determining more exactly the receptive-field of the reflex.

Receptive-field. This, Fig. I, 3, occupies practically the whole concavity of the concha and extends into the auditory meatus including the whole internal circumference of that: I have traced it into this latter for some 8 mm., the surface beyond that becomes inaccessible to isolated stimuli introduced through the orifice even in the shaven ear. It extends slightly over the lower part of the concavity of the scapha, there trespassing on the lowest zone of the retraction reflex of that part. The reflex is also elicitable by touches on the convex back surface of the concha over the ampulla region, but here the pressure of the touches has to be rather heavy, and it is possible that the excitation is by conveyance of the stimuli through the skin and concha to the deep concave surface. This receptive-field is completely ringed round by that of the retraction reflex.

Adequate stimulus. The nature of the adequate stimulus is clearly mechanical. Faradic stimulation applied with the precautions adopted for retraction-pinna reflex is found to evoke the head-shake reflex rarely and irregularly; it is far less effective than mechanical stimuli. As to mechanical stimuli, the lightest touch is often sufficient, *e.g.* a fine cotton thread 12 cm. long gradually lowered into the shaven ear so that its hanging end finally touches the supratragus or ampulla. Light drafts of air directed into the concha excite the reflex seemingly as readily, or almost so, in the shaven ear as in the unshaven; to excite the reflex it is sufficient merely to breathe out through a fine tube directed toward the concha even at a distance of 10 cm. away. Puffs of air too faint to evoke the retraction or folding reflexes are still easily able to evoke the head-shake reflex when directed to the concha. Whether in this case the stimulus is really mechanical or not is uncertain; its adequacy may attach to the slight cooling produced by the draught. But the draught produced by a breath even at the extreme end of a long expiration, *i.e.* with air warm and moist from the lungs, is still a completely effective stimulus. So also is air from a heated chamber, *e.g.* from the hot air chamber provided for artificial respiration in the Brodie experimental table. These stimuli when applied to my own ear were, however, felt by me as a slight coolness, even at greater distances than those from which they evoked the reflex in the preparation.

Trials with fluid indicate that one of the functions of the guard-hairs is to prevent ingress of fluid into the concha and meatus, for it is not easy to introduce water past them or to evolve the shake-reflex from them. But, of course, they are not effective against a large quantity, or against water squirted into the ear. When water does enter it acts as an extremely potent stimulus. Observations with the shaven ear gave the following results. A single small drop let fall into the concha from a height of about 1 cm. evoked the reflex, especially easily from lateral cushion and the immediate neighbourhood of the meatus; the greater the height of fall the stronger the reflex. A drop could sometimes be placed on the cushion without exciting it, but a larger quantity even so would provoke the reflex. A large drop placed on the edge of incisura medialis would not excite the reflex but when then allowed to run of itself down the groove into ampulla did excite. Oil excited the reflex less readily than water.

As to whether in such cases the stimulus is mechanical or thermal, oil and water warmed to the temperature of the finger and thermally imperceptible to my own finger or ear at the time still excited the reflex, but not so markedly as when cold (at room temperature) or hot, *i.e.* at 65°. A drop of warm water at a temperature yielding no thermal sensation to my hand has on several occasions after evoking the shake-reflex when first introduced gently into the concha evoked it again some seconds later when, so far as one could tell, simply lying in the ampulla. It is very difficult in such cases to understand how it can have acted as a stimulus either mechanical or thermal. A wisp of dry cotton wool lightly placed in the concha sometimes evoked the reflex. From these results it seems that the receptors although adapted to mechanical stimuli respond also to cold and heat as well. This point will be returned to in regard to the adequate stimuli for the pinnal reflexes as a group.

Electrical stimuli evoke the reflex with difficulty and unreliably.

Afferent nerves. The reflex persists after combined severance of the roots of trigeminus, octavus, glosso-pharyngeus, spinal accessory, hypoglossus (recently shown by J. Boeke(2) and Van Rynberk(16) to be a sensori-motor nerve) and the three headmost cervical nerves. It then disappears on severance of the vagus root, or of its two most posterior rootlets. Practically the whole area of the receptive-field is supplied by vagus fibres (Fig. II, xth), except the somewhat doubtful part of the field on convex posterior surface of the concha. But experiments by the remaining æsthesia method show that trigeminus (Fig. II, vth) and 1st cervical (Fig. II, 1st) roots contribute supply also to parts of the field. The branch of vagus responsible is presumably the 'auricular' twig. I have not cut this isolatedly. When the above nerve-roots including vagus have all been severed except trigeminus the reflex field is restricted to a part of the concha, especially the groove between the two cushions and the meatal orifice itself. The reflex is then extinguished by cutting the third division of the trigeminus. These trigeminus afferents run doubtless by the auriculo-temporal branch of the nerve's third division. Again, after severance of all the cranial nerve roots and of the 2nd and 3rd but not the 1st cervical, the reflex is obtainable from a small part of pinna where the concha meets the scapha just dorsal of the wart and along the deeper parts of the bursellar folds. I have not found evidence that any of the afferent fibres run in either the 2nd or 3rd cervical nerves. The main afferent nerve of the reflex is therefore the auricular branch of the vagus, the old sensory nerve of the original gill-slit which has been modified into the outer ear-passage. Although the main afferent nerve is vagal the reflex itself leaves the respiratory rhythm undisturbed.

4. *The cover reflex.*

This reflex very commonly accompanies the head-shake reflex. The movement made in it is a forward inclination of the whole pinna swinging it clockwise, as seen in the right pinna viewed from the right side, about an axis running transversely through the head between the external auditory meatuses. The pinna is at the same time somewhat flattened and broadened, and depressed in a fan-like fashion over the meatal entrance.

The pinna is also somewhat rotated about an axis running from the meatal orifice toward the pinna-tip, the direction of rotation bringing the latero-ventral edge of the pinna forward. At the same time the bursellar part of the scapha is somewhat everted, and the lower part of the orifice into the pinna is thereby narrowed. The motor-nerve is *facialis*. Also not unfrequently the animal rises on its fore-quarters and the neck is tilted upward.

Receptive-field. The field of skin from which the reflex can be evoked occupies practically the whole of the inner face of the concha, also the meatal orifice for its whole circumference to a depth of at least 8 mm. deeper than that I have not been able to apply isolated stimuli. The focal area of the field includes the wart and its immediate neighbourhood, the opposed faces of the cushions and the groove between them, and the actual entrance of the meatus. This field corresponds so nearly with the head-shake field that it has not seemed necessary to give a separate figure of it. When excited from the edge of its field the reflex may follow on a retraction-pinna or a crumpling reflex.

Adequate stimulus. Fluid, a draught of air, and mechanical touches are all provocative, but seem to be required in rather higher intensity than for the previously mentioned reflexes, especially the puffs of air. I have, however, seen a drop of water placed on the lateral cushion while not evoking the shake-reflex evoke the cover-reflex. Electrical stimuli in form of faradism applied as above mentioned evoke the reflex irregularly and with difficulty. In the part of the receptive-field which is hairy touching of the hairs evokes the reflex; so likewise touches after the skin has been shaven. The larger part of the receptive-field is hairless.

Afferent nerves. When vagus was the only nerve left uncut the reflex was still brisk practically from its whole field, and when the trigeminus alone was left uncut the reflex was still briskly obtained from the part of the field belonging to that nerve. On the other hand, when the vagus and trigeminus had both been severed, the 1st, 2nd and 3rd cervical nerves remaining either singly or altogether, in no experiment was the cover-reflex elicitable. The inference from this negative evidence is therefore that the cervical nerves although supplying part of the skin over which the receptive-field of this reflex extends do not contain afferent fibres mediating the reflex; it may be, however, despite the negative evidence of my experiments, that 1st cervical does contain fibres for it, as for the head-shake. The main afferent nerve of the reflex is clearly the auricular branch of the vagus. The reflex has analogies with the reflexes described for the gill-slit cover by Van Rynberk (17) and by T. Kuiper (11) and by S. Baglioni (1). No interference, however, with respiratory rhythm accompanies the pinna cover-reflex so far as I have observed in the cat.

5. *The scratch reflex.*

In the cat from the inner face of the conchal part of the pinna and from the auditory meatus, the scratch reflex can usually be elicited, and this is well seen in the decerebrate preparation. The movement is, of course, very different from those of the reflexes above described. As regards the hind limb and the curving of the trunk, etc., the muscular reaction both postural and rhythmic has been described already, but as regards the posturing of the head and neck it departs, when induced from inside the pinna, from the attitude assumed when evoked from the neck (22). In the former case the head is lowered and turned sideways, so as to allow the hind paw to reach the inside of the concha.

Receptive-field. This includes (Fig. I, 6, 7) the concavity of the concha and encroaches on that of the scapha above the upper part of the crescent. It also extends into the meatus. Besides belonging to the front face of the pinna it occupies the skin of the back of the proximal part of pinna as far as the border where the fur changes from longer hairs to shorter, this border seeming to mark there the actual limit of the receptive-field. It therefore does not include the distal part of the pinna either back or front. It runs backward from the root of the pinna over the neck and also slightly upon the scalp median to the medio-dorsal edge of the root of the pinna. It does not in my experience extend to the cheek. Focal areas of the receptive-field in the concha lie in the groove around supratragus, and at the meatus.

Adequate stimulus. Mechanical stimuli in the form of touches excite the reflex, occasionally even light touches on the inner face of concha at and above the supratragus, but not touches so light as those evoking the shake reflex from the concha, nor touches so light as those evoking the retraction pinna and crumpling reflex from their respective fields. Blowing into the concha or insertion of a drop of fluid fail to evoke the reflex: I have seen a very strong draught of air evoke it doubtfully. As to the part played by hairs in the receptive-field, a large part of the field is hairless, and in the part which is hairy, *e.g.* convex outer surface of concha, touches, rather heavy but seemingly not heavier than those usually required there to evoke the reflex, evoke it still when the skin has been carefully shaven. The mechanical stimuli adequate are therefore heavier than those required for the other reflexes and of the nature of pressure rather than touch: the pressure required seems lightest in the groove about supratragus. Rubbing the skin evokes the reflex powerfully. Also deep pressure with the finger tip just behind the back of the convexity of the concha.

This reflex differs markedly from the retraction pinna reflex in the relative ease with which faradism excites it. This is readily shown by unipolar faradism with the stigmatic electrode in the concha and the diffuse electrode on a fore-paw or the contralateral hind-paw.

Afferent nerves. The reflex is still readily evocable after all the afferent nerves except the vagus have been severed; auricular branch of vagus therefore contains a fair proportion of its afferents from this field. It is also obtainable after all the cranial roots behind trigeminus together with the headmost three cervical roots have been severed. In this case, however, only the meatal and deepest part of the ampulla reply. It is obtainable also when all the above roots have been severed excepting only 1st cervical, or only 2nd cervical, or only 3rd cervical, but in the case of the last two not from inside the concha, the field being restricted to the convex posterior surface of concha at the back of the pinna. This wide segmental distribution of the afferent fibres concerned with the reflex is borne out by the reflex being evocable by faradisation of the afferent root of the trigeminus and of afferent roots of 1st and 2nd cervical respectively. It can also be evoked by unipolar faradisation of the sectional face of the ascending (spinal) root of trigeminus (22, 3) in cross-sections of the bulb and headmost spinal cord.

6. *Inter-relations of the pinnal reflexes.*

Certain of these pinnal reflexes, though each under a moderately brief and circumscript stimulus commonly occurs alone, tend to occur together making a compound reflex response to a single stimulus. The retraction reflex and folding reflex are in this sense rather closely linked, so also the cover reflex with the head-shake. A strong stimulus evoking the head-shake sometimes evokes the scratch reflex also; and then occasionally it seems that there is inco-ordination for the hind-limb appears to move towards the head and make scratching movement while the head itself instead of being steadily turned back toward the advancing limb is still upturned and executing the rotational movement of the shake.

The retraction, folding, and cover reflexes of right and left sides are strikingly independent of each other. It is as easy to obtain them from the pinna of one side while that of the other side is itself exhibiting one of the reflexes as when the fellow ear is quiet. This is in marked contrast to the close inter-relation, usually inhibitory, between right and left reflexes of the neck and limbs.

7. *Comparison of the receptive-fields of the pinnal reflexes with the skin-fields of the cranio-spinal nerves of the pinna region* (Figs. I, II).

Study of these reflexes gives opportunity for seeing how far the functional unity of a receptive-field conforms with, or represents, the morphological unity of a segmental root-field. Comparison of the receptive-fields of the respective reflexes with the skin-fields of the several nerve-roots cranial and spinal distributed to pinna-region shows clearly that the factor which decides the central reflex connections of the afferent fibres of each root is the functional position of each portion of the skin the root supplies rather than any primitive morphological entity which each respective cranial or spinal nerve may be supposed to represent. This is evidenced plainly if the extents and borders of the reflex-fields shown in Fig. I are contrasted with the root-fields shown in Fig. II. No single root-field is identical with any single reflex-field; nor is any single reflex-field identical with any group of root-fields. There is not even approximate agreement between them. Even the vagus skin-field (Fig. II, xth), confined entirely to the concave face of the pinna (27), contributes to the head-shake and cover reflex below in the concha, but to the retraction and folding reflexes above where it extends over part of the scapha. Similarly trigeminus, where it is distributed over the cheek in front of tragus, intertragus and post-tragus, contributes fibres to the head-shake reflex and to the scratch reflex. Again, the 1st cervical nerve where it spreads into the concha supplies afferents for the head-shake, cover, and scratch reflexes, and where it spreads over the scapha and back of the pinna supplies afferents for the retraction reflex and the folding reflex. Comparison between the two sets of diagrams furnishes other instances of similar import, and no evidence in the other direction. The functional topography of the skin of this region is evidently not governed by the limits of the ancient root supply.

II. Vibrissal Reflexes.

The long vibrissæ of the cat's face are arranged in two groups, the one on the upper part of the muzzle above the mouth, the other superciliary. From the former in my experience no reflexes are clearly elicitable. From the latter reflex-closure of the eyelids is easily obtainable. In the decerebrate preparation a light touch on a superciliary vibrissa, displacing it even slightly, is often a sufficient stimulus.

As to the muzzle-vibrissæ, although in my experience reflexes are not readily or regularly evocable from them, movements of them not rarely accompany the retraction and folding reflexes of the pinna evoked, as above, from the pinnal region itself.

III. Jaw Reflexes.

1. *Jaw-closing reflex.*

Reflex closing of the jaw accompanies the reflex swallow which is so readily obtainable in the decerebrate preparation by putting a little fluid into the mouth (13). Reflex jaw-closing is also evoked as a movement by mechanical stimulation, *e.g.* by stroking with a feather the dorsum of the tongue near its tip. The tongue tip is curved slightly upward and somewhat retracted and at the same time the mandible is raised and the mouth rather deliberately closed and in the decerebrate preparation tends to remain so. This slow movement leads to no reverse action of opposite phase in the antagonistic muscles employed; it thus offers striking contrast to the jaw-opening reflex described below with its quick movement tending to be followed by strong reversal.

2. *Jaw-opening reflex.*

In the decerebrate preparation the jaw maintains a closed posture (19). This is in harmony with the rule (23) that decerebration brings all the anti-gravity muscles into steady reflex postural activity. With this steady posture as a background, stimuli applied to a rather restricted receptive surface evoke regularly in the decerebrate preparation the opening of the jaw. The surface in question is that of the gum bordering the teeth both of the upper and lower jaws, also the front part of the hard palate.

The reflex movement is quick and is followed immediately on withdrawal of the stimulus by a quick return to the previous closed posture. So quick and sudden is the opening and so sharply followed by active return of closure that, under electrical elicitation, the phenomenon at first suggests escape of the stimulating current to the motor nerve of the jaw-opening muscles. That the reaction is truly reflex can, however, be easily proved. (1) The induction currents cease to evoke it from the gum of the upper jaw as soon as the afferent nerve of that jaw (superior maxillary of trigeminus) has been cut, and from the gum of the lower jaw when the inferior dental nerve is cut. (2) The reaction is evocable by mechanical stimuli to the gum or teeth either of upper or lower jaw, and these stimuli likewise cease to evoke it after severance of the above afferent nerves. (3) In the freshly killed animal strong faradisation (unipolar or bipolar) of the gum upper or lower often produces strong closing of the jaw, but never opening of it. Current-escape therefore in this situation tends, as one would expect, to excite the near adjacent closing muscles and closure not opening is the result of current-escape. The jaw movement is accompanied by some retraction of the cheek and angle of the mouth, as if to keep the border of these out of the way of the bite.

Receptive-field and the stimuli. Blunt pressure, as for instance with the shaft-end of a small feather, on the gum bordering the crown of a tooth evokes the reflex. So also pressure on the tooth-crown often markedly evokes the reflex. These mechanical stimuli have to be much heavier than those sufficing for the pinnal reflexes. The gum border is not equally responsive for the reflex all along its length. It seems in my experience most responsive near the 2nd premolar teeth and least so at the canines. Faradisation evokes the reflex well. I have used this by the unipolar method. The stigmatic electrode excites the reflex not only when applied to the gum bordering the teeth but also when applied actually to a tooth. Here again the stimulus has acted best at the premolars, but even at the tip of a canine it will also often evoke a good reflex. Faradism also excites the reflex from points in the front part of the hard palate. Stimulation of the central stump of the severed superior dental branch of superior maxillary nerve likewise elicits the reflex.

After separating the halves of the mandible at the symphysis it is possible to see how far the reflex movement evoked, say from the premolars of one side, is bilateral or unilateral. The reflex is then found to be practically unilateral. Mechanical or faradic stimulation of the gum or teeth of the right side produces its reflex effect on the muscles of that one half of the mandible, and not unless the stimulus is quite strong is the other half involved as well. Even then the reflex effect on the contralateral musculature is feeble.

The opening muscles of the jaw, *e.g.* digastric, when exposed can be seen to contract in the reflex. This observation becomes particularly clear in these muscles after their detachment from the jaw in front. And if after their detachment, the head being prone and the split half of mandible still closed against the maxilla by reason of the decerebrate rigidity, the stimulus be applied, *e.g.* the stigmatic electrode brought to touch a premolar, the ipsilateral half of the mandible is seen immediately to drop. This occurs by reason of the reflex central inhibition of the jaw-closers: *temporalis, masseter,* etc. It can be ascertained in other positions of the head by light pressure against the mandible with the finger. The reflex therefore strikingly exhibits reciprocal innervation in its taxis of the antagonist muscles.

The reflex further exhibits strikingly the phenomenon of rebound (24, 25, 8) met with especially as a post-inhibitory reaction in the extensor muscles of the fore and hind limbs. On withdrawal of the stimulus, *e.g.* faradic, to the maxillary gum the temporarily relaxed jaw-closers immediately enter into a strong contraction relifting the split half of the mandible and shutting it tight, often with a powerful snap. It is to be noted that here just as in the fore and hind limb, the rebound-contraction is exhibited by antigravity muscles; the extensors, *e.g.* supraspinatus, vastocrureus, gastrocnemius being anti-gravity muscles in the limb in the same sense as are temporalis and masseter at the jaw. When the stimulus is strong the rebound appears to predominate and contraction of the closers may ensue earlier in the reflex.

This jaw reflex as thus evoked from gum, teeth, or hard palate is therefore, like the ipsilateral flexion reflex of a limb a diphasic reflex. The first phase, as excited at least by weak or medium strength stimuli, is opening of the jaw; the second which tends of itself to follow on the first is closure of the jaw. The ipsilateral flexion reflex of the limb in decerebrate rigidity and under slowly repetitive stimulations gives a stepping movement the flexion phases of the stepping occurring with each stimulation, the extensor phases occurring by rebound between the successive stimulations. Similarly the jaw reflex under a series of repetitive stimulations results in a masticatory movement, the openings of the jaw occurring with the stimulations, the closings by strong rebounds between the stimulations. From the prominence in this reflex of reflex central inhibition and the central rebound ensuent on that it would seem that in the rhythmic act of mastication in so far as concerns all that large part of it which it executed reflexly, and subject to the same reservations (26, 4, 5), just as in the rhythmic act of stepping, the rhythmic alternation of two active reflex phases is obtainable by the mere alternate recurrence and lapse of one single mode of stimulus. On the mouth's seizing a morsel the mandible, when it has closed, *e.g.* voluntarily, upon whatever is between the jaws pressing it against the gums and teeth and hard palate, by so doing, as is clear from observation of the reflex, produces a stimulus which tends reflexly to reopen the jaws. That done the central rebound of the previously reflexly inhibited jaw-closing muscles, or rather of their motoneurones, for the inhibition is central, sets in and tends to powerfully reclose the jaws again. The reclosure brings into operation once again the jaw-opening stimulus. And so, after being started by a first bite, a rhythmic masticatory reflex tends to keep itself going so long as there is something biteable between the jaws.

IV. Narcotics and the Reflexes.

The pinna reflexes emerge very early from the shock of decerebration and are submerged very late in chloroform or ether narcosis. They disappear often much later under chloroform than does the conjunctival reflex. Their suppression serves as a good index to complete chloroform narcosis, and I have been accustomed for a long time past to use them as such in the laboratory, thus obviating the necessity of removing the chloroform apparatus from the face in order to test the conjunctiva.

The jaw reflexes in my experience take longer to emerge from the shock of decerebration; but they can generally be elicited soon after the conjunctival reflex has appeared.

All the above reflexes can be demonstrated easily in the normal, *i.e.* not decerebrate, animal under various degrees of chloroform or ether narcosis. For the jaw-opening reflex faradisation of the gum is then more efficient than is mechanical stimulation (pressure, etc.).

V. Representation in the Cortex Cerebri of the Movements.

Recalling previous experience of stimulating the cerebral cortex in the cat and other animals, I could not remember having there met with the pinnal movements seen in the above reflexes of the decerebrate preparation. Nor on referring to the literature of the cortex do I find record of any such. I have therefore explored the cat's cortex again with special reference to them. The hemisphere was exposed under deep chloroformisation, and the surface then gone over point for point by unipolar faradisation. This was done in six animals. The various usual responses were obtained, flexion of fore-limb and of hind-limb, rotation of neck, retraction of angle of mouth, closure of contralateral eye, twisting of the nostril, opening of mouth, retraction of tongue, etc. The only movement of the pinna obtained was a slight protraction, a 'pricking,' not like any of the pinnal movements obtained as reflexes in the decerebrate preparation. This cortical movement was obtained from the coronal gyrus near the junction of that with supra-sylvian and close against the anterior supra-sylvian sulcus of Langley (12). This is the position originally noted by Ferrier (7) to yield in the cat "a drawing forwards and downwards of the ear." The movement was also, though irregularly, obtained from somewhat further lateral namely from a part of gyrus sylviacus anterior of Langley. The movement was one which protracted the pinna as a whole, not involving any separate movement of the tip or other parts. Of the reflex movements of pinna the one to which it bore some though not close semblance was that of the cover reflex, but the twisting and eversion of the bursella characteristic of this latter was not present in the cortical movement, nor was there the flattening of the scapha. This negative result was somewhat strengthened as evidence by the fact that the degree of etherisation which permits motor responses from the cortex permits also elicitation of the pinnal reflexes by stimulation of the pinna, so that these, *e.g.* retraction reflex and folding reflex, remained elicitable by mechanical stimuli of the pinna during the faradic exploration of the cortex. That the slight protraction movement obtained from the cortex had nothing to do with these reflexes was further shown by evoking a pinnal reflex and while that was in progress evoking the cortical movement of the pinna. The result was that the retracted and folded pinna was simply shifted forward as a whole, without either increase or diminution of the reflex engaging it. Nor did the occurrence of the reflex interfere with the obtaining of this cortical response.

The evidence is negative, but so far as it goes it asserts that the group of reflex movements, above described, elicitable so readily from the decerebrate preparation and also (*v. infra*) from the normal animal, are not represented in the cortex cerebri. As a rule movements of the skeletal musculature readily obtainable as spinal or cranial reflexes are also obtainable by excitation of the cortex (19), and are, indeed, preponderant among the cortical responses. A negative result in this respect is therefore not without interest.

The scratch reaction was also looked for in the cortex, and not found. From the hind-limb area of the cortex rhythmic flexion of the contralateral hind-limb including flexion of ankle was sometimes evoked, and on some occasions bore some resemblance to a feebly developed scratch-reflex response, but the characteristic flexion of the toes accompanying ankle-flexion was wanting, and the rhythm was too slow. Similar rhythmic alternate flexions and extensions of the fore-limb could at the same period of the experiment be evoked by shifting the electrode to the fore-limb area; these were evidently stepping movements. The inference was therefore that the hind-limb movement also was 'stepping' and this was borne out by the movement being evoked in fore and hind-limb together, and then flexion in one was seen to follow that in the other although agreeing in frequency. The exploration failed therefore to find the scratch reflex represented in the cortex.

But although the pinnal reflexes including the scratch could not be found the movement of eye-closure as elicited from the superciliary vibrissæ, and of jaw-opening as elicited in the jaw reflex were easily evocable from the cortex; and both are of course well-known among cortical reactions, the situation of their foci in the cat having been determined first by Ferrier (7). As elicited from the cortex the movement of opening of the jaw tends to be smartly followed by jaw closure as it is also in the decerebrate reflex. Also, just as after the mandibular symphysis has been split, the reflex is found to be practically unilateral, so is the reaction as provoked from the cortex, though in the latter case the muscular effect is of course contralateral in the former ipsilateral. There are however some evident differences between the cortical and the reflex reactions in the cat in regard to their muscular taxis. As obtained from the cortex the jaw opening is accompanied by retraction of tongue and it is often not easy to dissociate the two reactions. As obtained in the decerebrate reflex the jaw opening is not accompanied or is accompanied little and rarely by movement of the tongue. Again, the cortical reaction of jaw-opening, especially as obtained from low down in the anterior composite gyrus of Langley, tends to be the first phase of a rhythmic act of alternating openings and closings of the jaw (mastication). But the decerebrate reflex although it tends to produce a sharp closure ensuent on the opening does not under simple continuance of its stimulus develop a rhythmic succession of alternating movements.

In other words the reflex tends to exhibit a single complete bite; the cortical reaction a performance of mastication.

VI. Comparison of the Reflexes with Reactions in the Normal Animal.

After study of the above reflexes in the decerebrate preparation it was of interest to examine the normal cat's behaviour when touches, etc., are applied at various parts of the ear. With the animal comfortably seated on an assistant's lap the touches were applied with the ordinary æsthesiometer or with a small camel's hair paint brush. The stimuli evoked from the points touched the same movements as those described above in the purely reflex preparation; and they evoked no others, except that the animal at times became impatient and restless though for the most part it remained quiet, often purring. It would continue purring even when the attitude of the ear temporarily assumed was that indicative of anger as in the Darwin figure.

Summarising the results they were as follows. The retraction and the folding reactions were evoked about as readily as in favourable reflex experiments; that is, the threshold of excitation seemed as low, certainly no higher. They were evoked much more readily than in many of the reflex experiments. To apply touches isolatedly to some of the points in the ear one had to work with the ear cleanly and completely shaven. On several occasions then the touches evoked the retraction reaction when applied to concha below the crescent, a region lower than had been observed to yield the reaction in the reflex preparation. The shake reaction was likewise evoked about as readily as in favourable reflex experiments; the limits of its receptive-field seemed exactly the same as that delimited in the reflex preparation. A puff of air or a droplet of water evoked it with about the same readiness as under pure reflex conditions. The reaction, however, was usually more violent and more prolonged than for corresponding intensities of stimulus in the reflex preparation. It also had frequently a much longer latency. The cover reaction seemed the least readily induced. The scratch reaction was readily excited by its appropriate stimuli and from both divisions of its receptive-field, *i.e.* both from the front and from the back of the pinna. A prolonged touch by a blunt pencil on the concha of the shaven ear provoked it well, so also pressure with a wad of cotton wool. Just as in the reflex preparation there was a tendency for some of the several reactions to occur together in response to a single stimulus. Thus, retraction and folding reactions were often conjoined, and the head-shake along with the cover. Sometimes retraction reaction or folding reaction occurred along with the head-shake, the latter following on the former. Occasionally the scratch reaction and the head-shake were coupled together, but always in sequence, the sequence being head-shake, scratch and then head-shake again. The posturing of the head in the scratch reaction is antagonistic to, *i.e.* incompatible with, the movement it makes in the head-shake. Touching the superciliary vibrissæ caused closure of the eyelids as in the reflex preparation.

Differences noted between the reactions in the normal animal and those in the reflex preparation were the following. In the normal animal the receptive-field of the retraction and folding reactions extended somewhat further into concha. The shake-reaction was frequently slow in appearing as though the animal were not disposed to make it. The head-shake was usually a much more prolonged movement than in the reflex preparation. Occasionally when the cat, at a break in the examination, was placed on the floor to walk about, the first thing it did was to give the head-shake although just before while lying in the assistant's lap it had not given any response to a droplet of water placed in the concha; the reaction had then presumably been for the time being suppressed, but was permitted when the cat was set down on its feet in freedom. The scratch reaction often showed a very long latency, the cat seeming indisposed to permit it to ensue. When the movement appeared it was much more perfect and prolonged than in the reflex preparation. The two middle toes were put actually within the concha, whereas in the reflex preparation the foot very rarely actually reaches the head commonly beating in the air several cm. away from the pinna. In the normal cat a touch upon the muzzle-vibrissæ usually caused turning of the head toward the side touched, whereas in the reflex preparation very rarely is any movement at all evoked. In the normal cat a sound coming from the adjoining room would sometimes excite a slight lifting of both ears, a cocking of both pinnæ; this movement was quite different from any of the reflex ear movements met with in the decerebrate preparation; but from the cortex as Ferrier noted it is elicitable, though then in my experiments (*v. s.*) it appeared in one pinna only, the contralateral.

Any endeavour to elicit the jaw reflexes from the normal cat promised so little likelihood of reaching an unconfused result, owing to the requisite faradisation, etc., of the gum making the animal fractious, that I did not attempt it. Remembering, however, that the mucosa of the human cheek is practically devoid of nociceptors in the region of the second upper premolar (10), I tried on myself faradisation of that spot and its neighbourhood, by the unipolar method, with the stigmatic electrode on the mucous surface. When one does this with a fairly strong current one experiences an almost uncontrollable impulse to open the jaw wider. A form of electrode suitable for the purpose is that previously described (9) for work with the central nervous system, because the wire is sheathed with ebonite up to its tip, while the free end of the platinum being fused to a little bead and the platinum itself carried by a light spiral spring, the mucosa though easily steadily pressed on, cannot be pricked. A convenient way of making the observation is with one hand to bring the tip of this electrode through the open mouth to the gum and then while the interrupter of the inductorium is running and the secondary circuit unbridged, to dip the other hand in a basin of salt water in which the diffuse electrode has been placed.

VII. Nature of the Adequate Stimuli and the sensations.

Of questions raised by these reflexes one concerns the intimate nature of their adequate stimuli. For human touch-spots the progress of research has gradually traced the nature of the adequate stimulus to be local deformation of the skin surface. This analytic result can answer obviously for those stimuli of the cat's pinna or vibrissæ which move the hairs or hairlets, or consist in mechanical touches by the æsthesiometer, etc. But it is difficult to apply it to explain the operation of such stimuli as a faint puff of air directed upon the cleanly shaven skin, or into the hairless concha; or to such as a droplet of oil or water gently placed practically without impact upon them.

Yet if these latter act as thermal stimuli the thermal receptivity must be extremely acute, for they still act when warm at a temperature imperceptible to one's own finger and ear, though of course one cannot be sure that the temperature of these latter and of the cat's pinna in the experiment are the same. The problem recalls one that is raised by the swallowing reflex (13). There are a few drops of water warmed to the temperature of the tongue and placed on the back of the dorsum in quantities as small as ·2 c.c. excite in the decerebrate preparation the swallow reflex from a mucous surface, already wet with saliva. There also it was shown that the stimulus, whatever its intimate mode of operation, is of mechanical quality.

Another question raised is the species of sensation excited by the stimuli adequate for these reflexes when applied not in the decerebrate but in the sentient animal, in short the modality or modalities of sensation which is or are adjunct to these reflexes. For the human skin four species of sense are recognised, touch, warmth, cold, and pain. Of these it is well known that pain is closely bound up with bulbar and spinal reflexes, touch hardly at all. 'Pains' are, so to say, 'subcortical'; 'touches,' 'cortical.' The stimuli adequate for these pinna reflexes do not resemble the stimuli adequate for nociceptors (pain receptors), but do resemble and are practically identical with those adequate for human touch. In the cat's pinna there seems therefore to be a group of touch reflexes, bulbar and spinal. But touch on the general surface of the cat's body—except for the scratch reflex zone—is as impotent to excite spinal reflexes as it is in man. If one applies to one's own pinna the stimuli adequate for the cat's pinnal reflexes one notes that the sensations they evoke although tactual are tactual of a distinctive kind, quite apart from local signature, etc. They are not of neutral affective tone, which is to say, devoid of affective tone; they are all of markedly negative affective tone, which is to say, all distinctly disagreeable. The inference is therefore that in the cat among the modalities of cutaneous sense and among the species of skin receptors, there is one intermediate between pain and touch, between nociceptive and tangoceptive, probably nearer to touch than to pain. It might be termed 'affective touch.' As regards the stimuli adequate for this intermediate species, its receptors resemble the tangoceptors not nociceptors, yet like nociceptors they are closely and potently attached centrally to motor mechanisms in the bulb and cord; yet they are not, as nociceptors are, closely attached to the bulbar vasomotor and respiratory centres. Whether this intermediate form in the cutaneous series amounts actually to a separate species and modality further research must decide; it is partly a matter of name; receptivity suggests no, the reflex connections suggest yes, and the sensual experience tends to support the latter.

Summary of Conclusions.

A number of reflexes are elicitable from the pinna of the cat. The decerebrate preparation gives facility for observing these as pure reflexes. Their movements are protective of the pinna: some, the retraction and folding reflexes, seem directed against irritant touches, *e.g.* the settling of flies, etc., or against exposure to injury in fighting; others, the cover and head-shake and scratch reflexes, against the ingress of foreign matter, including water, dust, or insects, into the meatus and its ampulla.

The threshold of the mechanical stimuli exciting these reflexes is extremely low; on the other hand, the reflexes with the exception of the scratch reflex are excited with difficulty and uncertainty by electrical stimuli. The reflexes although connected eminently with the hairs are connected also with other skin receptors separate from the hairs. Some of the stimuli may be thermal.

The constancy of response and the low threshold obtainable in these pinnal reflexes allow minuter observations which tend to question the probability that the intimate nature of the mechanical stimuli 'adequate' for them can, as is generally accepted for human 'touch,' be subsumed under the rubric 'local deformation of skin surface.' The modality of sense attaching to them in the normal, *i.e.* sentient, animal is probably best stated as 'affective touch.'

The afferent nerve-fibres concerned with each of these reflexes are supplied from several segmental nerve-roots, among them the vagus. The afferent nerve-roots of the reflexes taken as a group are those of trigeminus, vagus, and 1st, 2nd, and 3rd cervical nerves.

The afferent nerve-trunks respectively involved evoke the retraction and the folding reflexes better when stimulated mechanically than when stimulated electrically.

No one of the reflex receptive-fields is identical with the skin-field of any one of the segmental nerves carrying its afferent fibres.

The superciliary vibrissæ evoke reflex closure of the eye; the maxillary vibrissæ evoke no reflex in the decerebrate preparation.

Mechanical and electrical stimuli applied to the gum, or teeth, both of the maxilla and mandible, or to the front part of the hard palate evoke reflex opening of the jaws followed by rebound closure; the reflex is preponderantly unilateral.

Exploration of the cortex cerebri finds large representation of the jaw-opening reflex and of the superciliary reflex but no evidence of any cortical representation of the group of pinnal reflex movements.

All the reflexes are easily obtained under narcosis. The pinnal and superciliary reflexes are also readily elicitable in the normal animal, their threshold of excitation by the adequate stimuli being then somewhat lower than in most though not than in all decerebrate preparations.

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